The Eyes of Chrysochloris hottentota and C. asiatica.

By
Georgina Sweet, D.Sc.,
Melbourne University.

With Plate 6 and 1 Text-figure.

Introduction.

After the completion of my work on the eye of Notoryctes typhlops, the opportunity was afforded me, through the kindness of Professor R. Broom, of Victoria College, Cape Colony, of examining the eyes of Chrysochloris hottentota and C. asiatica, which are herein described. I wish, therefore, to thank Professor Broom for my whole supply of material consisting of—

One adult, labelled Chrysochloris (Amblysomus) hottentota, Smith.

Two heads of same.

One, three-quarter grown, labelled C. asiatica, L. = C. capensis, Shaw = C. aurea, Pullar.

Two young of same: (A) newly born, (B) somewhat older.

The adults of C. hottentota and C. asiatica were retained as specimens, those two forms being not otherwise represented here.

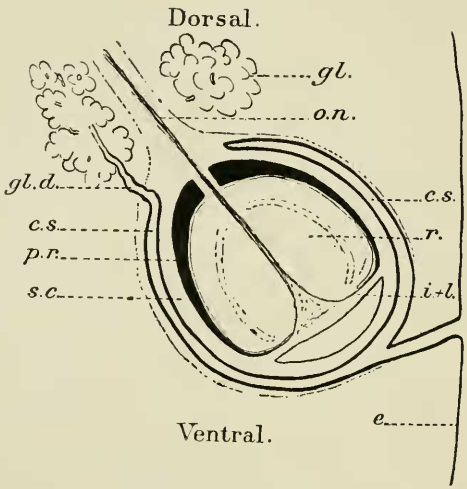
I have also, again to thank Professor Baldwin Spencer for the use of the Biological Laboratory in the University of Melbourne, where this work has been done.

I. C. hottentota. Adult.

The eyes of this species are situated in the dermis, between the roots of the hairs which surround the eyeball, while

beneath it are the subcutaneous muscles (see Pl. 6, fig. 1). Its general relationship may be seen on reference to the text-figure on this page. It lies at a depth of ·138 mm. below the surface, i. e. measured from the front of the sclerochoroid.

Its muscles have quite disappeared. Between the subcutaneous muscles at a short distance behind and on the inner side of the eyeball, is a large serous gland (Pl. 6, fig. 1, *gl.*), the lachrymal.



Text-figure 1.—Diagram of a section through the eye of Chrysochloris. *c.s.* Conjunctival sac. *e.* Epidermis. *gl.* Gland. *gl.d.* Gland duct. *i.&l.* Iris and lens. *o.n.* Optic nerve-fibres. *p.r.* Pigment layer of retina. *r.* Retina. *c.s.* Sclerochoroid.

The duct of this gland opens into the extreme ventral part of the conjunctival sac. This sac which is quite slit-like, passes almost completely round the whole eye, being absent at the back of the eye only (Pl. 6, figs. 1 and 2, *c.s.*). It communicates with the exterior by a narrow tube almost straight and running outwards, making an angle of 90° with the median longitudinal line of the eyeball, i. e. upwards and backwards. This tube, of course, represents the almost fused eyelids.

The conjunctival sac is lined by a stratified epithelium of two or three layers, similar to that covering the surface of the body (Pl. 6, figs. 1 and 2, *c.*).

The eyeball consists in general of the usual parts found in such degenerate eyes, representing the normal structures of an adult functional eye.

In length, antero-posterior diameter, the eyeball is ·51 mm., its transverse diameter being ·42 mm.

The fibrous sclerochoroid (Pl. 6, figs. 1 and 2, *s.c.*) is well developed, the front part of the choroid being somewhat less compact than the hinder. The retinal pigment layer (Pl. 6, figs. 1 and 2, *p.r.*) is very well defined; its epithelium of large cubical cells with slightly-staining nuclei almost completely surrounds the eyeball lying just within the sclerochoroid. Its pigmented area is considerably restricted being only present in the posterior one third of the eye, where, however, it has a considerable thickness. It extends somewhat further forwards on the ventral wall of the eyeball (Pl. 6, figs. 1 and 2). There is, however, a gap in the retinal pigment layer posteriorly, nearly in the median longitudinal line, this indicating the region of exit of the optic nerve (Pl. 6, fig. 2, *g.*). The bending in of the pigment epithelium to become continuous with the nervous layers of the retina is very well defined, taking place at about one fifth of the length of the eye from the anterior or outer end. In front of this reflexion, a well-marked structure passes right across the eyeball, leaving an anterior chamber quite separated from the posterior chamber which latter is quite filled with the retina. This degenerate iris (Pl. 6, figs. 1 and 2, $i + l$) arises from the inner layers of the sclerochoroid. It is thin around its origin, but swells out in the centre where it contains an irregular mass of cells in a fibrous-looking matrix; this is evidently the degenerate lens. The rest of the iris consists of a more crowded layer of cells anteriorly, and an areolar layer in the middle.

As the retinal pigment layer passes towards the median longitudinal line of the eye and almost at right angles to it, it becomes associated with a blood-vessel (Pl. 6, fig. 2, *b.v.*)

lined with flattened cells, and branching slightly in the retina. This is also in close relation with the internal fibrous layer of the retina, and with a more or less defined group of ganglion (?) cells. The remaining layers of the retina are comparatively clearly defined, the inner nuclear layer and inner molecular layers are hard to separate, but otherwise the nerve fibre, outer moleculæ, outer nuclear, and rod and cone layers are all well seen (Pl. 6, fig. 2). The internal and external limiting membranes are often very distinct. The layer of rods and cones separates easily from the pigment layer, owing to the great shrinkage of the retina which takes place after death or during preservation or preparation. Indeed, it appears to me that there may be, in life, a small posterior chamber occupied by some more fluid material than the ordinary vitreous humour contained therein.

In the outer layers of the retina, just opposite the gap in the pigment layer, is a similar space for the exit of the fibres to form the optic nerve.

Dorsally to the median line, the whole retina except the pigment layer is attached to the iris, otherwise lying freely in the optic ball, but passing ventrally the retinal mass is seen to lose this connection and become associated with the back of the eyeball. Near the median line of this area the sclerochoroid and the fibrous layer behind the conjunctival sac begins to be drawn (Pl. 6, figs. 1 and 2), so that the eyeball and surrounding fibrous layer has here a more pear-shaped structure.

At about the same horizontal plane the anterior chamber of the eye is lost, the iris having merged into the wall of the eyeball. Somewhat more ventrally to this again the gap in the pigment and outer retinal layers at the inner end of the longitudinal median line of the eye becomes much bigger and more definite; through it there passes backwards a bundle of optic nerve-fibres. This runs out and down the middle of the fibrous stalk of the now pear-shaped eyeball, this fibrous layer, as it tails out, forming the sheath of the optic nerve.

II. C. Asiatica. (*a*) Younger Embryo.

Here the eye lies in the subcutaneous connective tissue, immediately below the dermis and its hair-roots. It is 24 mm. below the surface at its nearest point to the latter.

The usual eye-muscles and associated nerves appear to be quite absent. A small, ill-developed gland is present inside the dermis, close behind the eye, but I was not able to trace any connection between it and the conjunctival sac. The cavity of the latter is represented by a very much reduced hemispherical space, in front of the eyeball. Its external tube does not run direct to the surface, or at right angles to the anterior face of the eyeball, but coils slightly and runs in an oblique direction to the surface, so that light could not penetrate to the bottom of it, unless in a very diffused form.

In size the eyeball is, in its antero-posterior diameter, ·48 mm., in transverse diameter ·30 mm.

The sclerotic and cornea are again quite similar and not to be distinguished from a choroid—all these three parts are represented by a thin fibrous capsule, which shows no trace of cartilage or pigment at any point. The retinal pigment layer lying immediately within the sclerochoroid is very thick-walled posteriorly, and gradually becomes thinner till, at the anterior part of the eyeball, it is absent for a small space, which may be regarded as the potential pupil. No cellular structure can be seen in the main mass of the pigment.

At the anterior end the reflexion of the pigment layer to become continuous with the rest of the retina is very clear. The space thus left in the middle line anteriorly is occupied by (1) a layer of columnar cells immediately within that part of the sclerochoroid representing the cornea; (2) within this in the middle line is a group of rounded cells bounded by a fine membrane; (3) on either side of this group is a double layer of extremely flattened cells leading out towards the pigment epithelium and sclerochoroid; and (4) immediately

behind (3) are a few irregularly arranged cells. Of these (1) appears to represent the outer layer of the iris; (2) this group of cells is evidently a degenerate lens; (3) is the remnant of the inner layer of the iris and the group of cells; (4) appears to represent some ganglion cells. Within the pigment ball lies the mass of retinal cells, showing very little differentiation into layers, and completely filling the cavity of the eyeball, there being visible no vitreous humour or lens (other than perhaps the group of cells mentioned above).

The outermost layer of cells is very densely packed, the cells having deeply-staining nuclei being apparently the outer nuclear layer. Between this and the pigment layer, and generally embedded in the latter, is a clear, almost homogeneous layer, probably representing the degenerate layer of rods and cones.

Within the outer nuclear layer the cells are much less closely packed, especially in the centre of the mass, but no clear division into the usual layers is present.

Along the median antero-posterior line is an irregularly double line of much flattened cells, associated with a thin fibrous layer, possibly representing internal limiting, and hyaloid membranes with nerve-fibre layer—the vitreous cavity being lost. No definite nerve-fibres are visible.

(*b*) Older Individual.

In this specimen the eye does not vary to any remarkable extent from that of the younger forms. Its depth below the surface is greater than in (*a*), being ·54 mm., though it appears relatively less deeply situated, owing to the greater depth to which the hair-roots extend.

The conjunctival sac extends almost completely round the eyeball, being only absent at one spot on the postero-ventral aspect—no doubt representing the place of exit of the optic nerve. Its walls are much more fibrous than in (*a*). The sac does not appear to open to the surface in one eye of this

embryo, its duct towards the exterior extending only a very short distance in front of the sac. That belonging to the other eye is, however, much more well-defined, and has a duct clearly leading on to the surface of the head. I have been unable to find any gland in this stage.

The eyeball is somewhat more elongated than that in the younger stage, being ·62 mm. in antero-posterior diameter, and ·44 mm. in transverse diameter.

The fibrous sclerochoroid is similar to that previously described, except that it is more strongly developed, and the choroid portion is less densely fibrous than the sclerotic part. The retinal pigment epithelium is well defined, though its pigmented area, as in C. hottentota, is in one eye (left) of this young individual much less extensive than in (*a*), being confined entirely to the posterior half, except in the median longitudinal line, where it extends round the front also. In the other eye (right) of this specimen the pigment is much more abundant, being only absent from the layer of pigment cells over a small circular area at the anterior end of the eye, much as in (*a*). In both eyes this pigment cell layer is absent in the median longitudinal line posteriorly, as in C. hottentota.

At the anterior end of the eye in this stage also the continuity of the pigment layer with the other layers of the retina is clearly seen, the reflexion taking place at about one sixth of its length from the front of the eye.

Passing over the anterior face of this layer is a membrane representing probably both internal limiting membrane and hyaloid membrane. This is continued back along the median longitudinal line to the level of the posterior gap in the pigment cell layer. There are associated with it remnants of optic nerve-fibres, but these are extremely indefinite, and are not continued outside the eyeball, there being no semblance of optic nerve.

At the anterior end of the eye, filling the triangular space which is left in the median line in front of the reflexion of the pigment layer, and which one may regard again as the

pupil, is a mass of cells and fibrous tissue irregularly arranged. This is the much more degenerate iris and lens.

The retinal layers have completely filled the greater part of the eyeball, so that in section the internal limiting and hyaloid membranes from either side are seen to be in contact along the median longitudinal line of the eyeball, there being no vitreous humour or posterior chamber. In more favourable parts, the outer nuclear, outer molecular, and inner nuclear layers are clearly to be seen, but the remaining layers are very ill-defined. No special ganglion cell layer is observable.

Outside the outer nuclear layer is an irregular, staining very faintly indeed, but often visible where the retina is torn away from its pigment layer. Distorted rod-like structures may be detected here and there in this, which is evidently all that is left of the layer of rods and cones.

(*c*) Adult.

The eye of the adult of C. asiatica lies as usual in Chrysochloris in the dermis among the roots of the hairs which surround the eyeball, while beneath it are the subcutaneous muscles.

The distance of the anterior face of its corneal region from the surface is ·51 mm. The length of the eyeball is ·54 mm., and its transverse diameter ·38 mm.

Its gland mass is much more deeply situated than in previous forms, the gland duct to the conjunctival sac being wide and very definite. No tube was to be found with certainty opening to the surface, but in view of the well-developed character of the gland-duct and conjunctival sac, and of the fact that no other exit was apparent for the excretion, it is probable that it was torn or distorted in some way during preparation, so hindering its detection.

In almost every detail otherwise, the eye of the adult of C. asiatica is closely similar to that of C. hottentota.

Summary of Structure.

1. The eye has sunk only into the dermis being surrounded by the hair-roots.

2. The conjunctival sac is well developed and also generally the lachrymal gland, the duct of which opens into the sac. From the sac, in most cases a cylindrical tube leads to the exterior. This tube, however, from its direction and sometimes coiling, can be of no use as a path for light rays giving rise to vision.

3. The eye muscles are quite absent.

4. Sclerotic cornea and choroid are represented by the fibrous sclerochoroid.

5. Lens and iris are very degenerate though recognisable. The vitreous humour is absent.

6. The pigment layer of the retina is thick posteriorly, and absent anteriorly.

7. The retinal layers are, in most cases, clearly distinguishable, very little degeneration being apparent in the outer ones. The layer of rods and cones is more or less distinct.

8. The optic nerve is present in some, viz. the two adults and older immature form, though the ganglion cell layer is the most degenerate part of the retina.

Comparisons and Conclusion.

As regards the position of the eye, that of Chrysochloris, while not generally visible from the exterior, even after shaving off the hair, as it is in Scalops (Slonaker, p. 335) and Talpa (Kohl, '93, '95, p. 13), is still comparatively superficial in contrast to that of Rhineura (Eigenmann, '02, p. 535) and Notoryctes (Sweet, p. 549).

The eye muscles are here absent, in contrast to most other burrowing forms, e.g. Scalops, Talpa (loc. cit.), Typhlops (loc. cit., and Kohl, '92, p. 124). The space between the conjunctival layers and between the eyelids is repre-

sented by the conjunctival sac, and generally a cylindrical tube to the exterior, as in Scalops, Talpa, etc.

The gland mass is generally well developed, as in Typhlops (loc. cit., p. 119, etc.), and Notoryctes (loc. cit., p. 551, etc.), its ducts opening into the reduced conjunctival space. Instead of the secretion being passed into the mouth as in Typhlops (loc. cit., pp. 119—121), or the nose, as in Notoryctes (loc. cit., pp. 552—554), it here usually runs out to the exterior directly through the "eye-cleft" as in Scalops and Talpa.

The sclerochoroid is similar to that in other degenerate eyes. The iris and lens are much more degenerate than in Scalops (loc. cit., Pl. 18, fig. 5, and Pl. 19, fig. 9), Talpa (loc. cit., p. 26, and Taf. III, figs. 27, 28, etc.), or Typhlops (loc. cit., Taf. VIII, fig. 84), but greatly less so than in Notoryctes (loc. cit., p. 559), where they are not recognisable as such at all.

The pigment layer is apparently not reinforced by degeneration to any great extent, and, as in most degenerate vertebrate eyes (except Notoryctes, Troglichthys [Eigenmann, '99(1), p. 581], and Typhlomolge [Eigenmann, '99(2), p. 53], etc.), is thickest behind, and more or less absent in front.

The retina is much more highly developed than one might expect from the condition of the lens, iris, etc.

The variability so often shown by degenerating structures is very evident here, not only between individuals, but also between opposite sides of the same individual, e. g. in the degree of pigmentation present in the retinal pigment layer, in the length and clearness of the optic nerve-fibres, and in the completeness of the severance of the connection with the exterior.

In comparing the eye of Chrysochloris as a whole with that of Talpa, Scalops, and Notoryctes, it may be stated in general terms that it is distinctly more degenerate than the eye of Talpa or Scalops, but very much less so than that of Notoryctes.

It is interesting to note that placing the individuals herein

investigated in order of degeneration, we find that the adults of C. hottentota and C. asiatica are the least degenerate, the intermediate stage of C. asiatica being the most degenerate in nearly every respect.

The eye of Chrysochloris is, without doubt, of no use for vision, even were the eye-cleft at the proper angle to admit light-rays in the proper direction, i. e. along the optic axis, and it is improbable that even degrees of light can be detected by it. At this stage of degeneration the gland secretion can have only its usual function of keeping the conjunctival cavity free from foreign matter.

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I regret that I have been unable to consult any literature on Chrysochloris other than one or two purely systematic papers, the valuable work done by other workers on this animal not being obtainable in Australia.

EXPLANATION OF PLATE 6,

Illustrating Miss Georgina Sweet's paper on "The Eyes of Chrysochloris hottentota and C. asiatica."

Reference Letters.

b.v. Blood vessel. *c.* Conjunctiva. *c.s.* Conjunctival sac. *d.* Dermis. *e.* Epidermis. *g.* Gap for optic nerve. *g.h.* Group of hairs. *gl.* Gland. *gl.d.* Gland-duct. *i + l.* Iris + lens. *i.n.l.* Inner nuclear layer. *m.* Muscles. *o.m.l.* Outer molecular layer. *o.n.* Optic nerve fibres. *o.n.l.* Outer nuclear layer. *p.r.* Pigment layer of retina. *r.* Retina. *r.c.* Layer of rods and cones. *s.c.* Sclerochoroid. *s.o.n.* Sheath for optic nerve.

All figures were drawn with the aid of the camera lucida.

Fig. 1.—General view of dermis of C. hottentota with eyeball, showing relations of latter.

Fig. 2.—More highly magnified view of eyeball of C. hottentota, showing more detailed structure. Compiled from several consecutive thin sections.